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MAINTENANCE OF PHENOTYPIC VARIATION IN PLUMAGE COLOURATION IN A PASSERINE BIRD

by

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LIST OF ORIGINAL PAPERS

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I Laaksonen, T, Sirkiä, PM, Calhim, S, Adamík, P, Artemyev, AV, Belskii, E, Both, C, Bureš, S, Burgess, M, Doligez, B, Forsman, JT, Grinkov, V, Hoffmann, U, Ivankina, E., Král, M, Krams, I, Lampe, HM, Moreno, J, Mägi, M, Nord, A, Potti, J, Ravussin, P-A and Sokolov, L. Character displacement and gradual change in plumage traits of the pied flycatcher. *Manuscript.*

II Sirkiä, PM, Adamík, P, Artemyev, AV, Belskii, E, Both, C, Bureš, S, Burgess, M, Bushuev, AV, Forsman, JT, Grinkov, V, Hoffmann, D, Järvinen, A, Král, M, Krams, I, Lampe, HM, Moreno, J, Mägi, M, Nord, A, Potti, J, Ravussin, P-A, Sokolov, L and Laaksonen, T. Spatial variation in selection on multiple male colouration traits in a passerine bird. *Manuscript.*

III Sirkiä, PM, Virolainen, M and Laaksonen, T. 2010. Melanin coloration has temperature-dependent effects on breeding performance that may maintain phenotypic variation in a passerine bird. *Journal of Evolutionary Biology,* 23, 2385–2396.

IV Sirkiä PM, Virolainen M, Lehikoinen E and Laaksonen T. Fluctuating selection and immigration as determinants of the phenotypic composition of a population. *Submitted manuscript.*

V Sirkiä, PM and Laaksonen, T. 2009. Distinguishing between male and territory quality: females choose multiple traits in the pied flycatcher. *Animal Behaviour,* 78, 1051–1060.

1. INTRODUCTION

The theory of evolution by natural selection provides us with an understanding of the broad phenotypic variation that occurs in nature (Darwin 1859). Information as to the evolutionary processes that influence current and future biodiversity is essential, particularly at times of rapid anthropogenic disturbances. The extent of variation in a population is crucial for current and future evolution, and it is thus of great interest to understand the mechanisms maintaining variation. The extent of heritable phenotypic variation in a population is for example the first step in speciation, and affects the evolutionary potential of populations to respond to environmental changes such as climate change.

The observed phenotype is the result of interaction between the individual's genotype and the environment. If a certain phenotypic trait is mainly driven by environmental factors, phenotypic variation in a population can be maintained by spatial and temporal alteration in environmental conditions. Natural selection is expected to act on phenotypic traits that are linked to fitness (Fisher 1930), and genetic variation in a fitness-related trait is expected to erode rapidly due to directional selection. One of the largest unanswered questions in evolutionary biology is the persistence of variation in fitness-related traits (Tomkins et al. 2004). Two broad explanations for the maintenance of such variation are mutation-selection balance and fluctuating selection. In mutation-selection balance the question is whether mutations can generate new variation as quickly as it is eroded by selection (e.g. Rowe and Houle 1996, Tomkins et al. 2010). In contrast, fluctuating selection is based on the idea that the performance of different individual types varies across environmental conditions in both time and space – a type advantageous in one environment may not be optimal in another. These genotype-by-environment interactions on fitness-related traits are common in free-living populations (Roff 1997), and can play an important role in maintaining phenotypic variation (Gillespie and Turelli 1989, Ellner and Hairston 1994). Selection on phenotype can alter in different contexts, and different phenotypes may be favoured under different conditions (Kassen 2002, Byers 2005, Roulin et al. 2008b, Bell 2010). In general, varying selection seems to play a significant role in the maintenance of variation in traits on both spatial and temporal scales (e.g. Siepielski et al. 2009, Cornwallis and Uller 2010). In addition, several mechanisms – such as frequency-dependent selection, heterozygote advance, antagonistic pleiotropy and mating with dissimilar individuals – are mechanisms that can contribute to the persistence of phenotypic variation (see further e.g. Futuama 1998). In this thesis I focus on the role of variable selection and its consequences as a factor maintaining phenotypic variation in male plumage colouration in a passerine bird, the pied flycatcher (*Ficedula hypoleuca*).

1.1 Different modes of selection maintain variation

Broadly speaking, selection occurs among phenotypic variants on the basis of survival and the ability to produce fecund offspring (Endler 1986). For selection to occur, at least two conditions have to be fulfilled. First, variation has to occur in some trait that is at least partly heritable. Second, constant fitness differences have to occur related to that particular trait. The relationship between phenotype and fitness has been traditionally divided into three different types of selection: directional, stabilising and disruptive selection (Futuama 1998). In addition, different modes of selection can be described based on the life-history stages during which selection is acting. In this thesis I focus on the role of sexual selection and natural selection acting through fecundity on the pied flycatcher male phenotype. Sexual selection arises as a consequence of competition for access to mates (Andersson 1994), whereas fecundity selection arises from differences in the number of viable offspring produced (Futuama 1998). Different components of fecundity, such as clutch size or number of offspring, may be affected by several different factors, such as parental quality, genetic effects, and varying environmental conditions.

Sexual selection consists of intrasexual selection and intersexual selection (Andersson 1994). In intrasexual selection, individuals of the same sex compete among themselves for access to reproduction. Males, for example, may compete for a territory, which is often a requirement for pairing in territorial species. In contrast, in intersexual selection the choice occurs between the sexes: for example females may choose among several males. Individuals are often particular in their mate choices, indicating that the decision has powerful fitness consequences (Andersson 1994, Jennions and Petrie 1997). Mate choice can carry both potential direct benefits, such as protection, access to resources or paternal care (Danchin et al. 2008), and indirect genetic benefits (reviewed in Kotiaho and Puurtinen 2007). The two components of sexual selection, intra- and intersexual selection, can interact with each other in several ways (e.g. Qvarnström and Forsgren 1998, Wong and Candolin 2005, Kotiaho and Puurtinen 2007, DuVal and Kempenaers 2008), and their effects are usually difficult to distinguish. For example female choice may be based on male characteristics, but also on characteristics of the territory that the male has gained by his success in male-male competition.

1.1.1 Trade-offs between fitness components and selection on multiple traits

Selection involves a number of components acting on a phenotype, and trade-offs can occur between different components of fitness. Different selective forces can act either in parallel or opposing directions, either simultaneously or at different life-history stages. Divergent selection pressures between different life-history traits have been suggested to be relatively common in free-living populations (Schluter et al. 1991). Opposing selection can lead to evolutionary trade-offs, which can constrain the response to selection and can contribute to genetic variation (Schluter et al. 1991, Roff 1997). It is often suggested that phenotypic variation in selected traits is maintained by a balance between different components of selection (e.g. Grant 1990, Delhey et al. 2003, Robinson et al. 2006).

The phenotypic traits of an individual are often inter-correlated, and selection also acts simultaneously on multiple traits. In general, the response to the net selection acting on a trait depends on its genetic correlation with other traits, which may be subject to different selection pressures (Merilä and Björklund 2004). The role of selection on correlated traits in the maintenance of phenotypic variation can be complex. The pleiotropic effects of a single gene, for example, can affect several apparently unrelated features of the phenotype and may drive covariance between different phenotypic traits. On the other hand, for instance sexually selected traits are frequently expected to be dependent on the body condition of an individual (Andersson 1994) which further can be affected by several different factors. In mate choice the simultaneous use of multiple cues seems to be relatively common, and may improve the accuracy or reduce the costs of assessing the quality of the potential partner (Møller and Pomiankowski 1993, Johnstone 1996, Candolin 2003). Information gained from different cues may differ in value for different individuals and in different contexts (Møller and Pomiankowski 1993, Candolin 2003). In general, mate choice acting on multiple traits has been suggested to be able to maintain phenotypic variation (Candolin 2003).

1.1.2 Spatial variation in selection

The evolutionary significance of spatial phenotypic variation has been known for decades (Mayr 1942, Mayr 1970, Zink and Remsen 1986). Local environmental and ecological conditions are expected to result in local adaptations, via processes of selection and microevolutionary change. Spatial variation in selection also maintains variation in phenotypic traits between populations (Endler 1980). It should be kept in mind, however, that in addition to selection, spatial variation between populations may also be due to genetic drift and phenotypic plasticity; thus variation as such does not prove selection (Zink and Remsen 1986, Newton 2003, Alho et al. 2010). Although selection has frequently been shown to vary spatially (e.g. Endler and Houde 1995, Fairbairn and Preziosi 1996, Blanckenhorn et al. 1999, Gosden and Svensson 2008, Weese et al. 2010), relatively few studies have been able to study variation in selection pressures directly over large spatial scales (Møller et al. 2006a), and our understanding of patterns of selection on phenotype across continent-wide spatial scales thus remains relatively poor.

In environment-contingent selection, scale is important in considering the maintenance of variation within and between populations. Adaptation to local conditions and gene flow between locally adapted populations can be seen as opposing forces (e.g. Nosil and Crespi 2004). Gene flow between locally adapted populations can reduce variation among populations, but may increase and maintain variation within a particular local population. In theoretical work, genetic variation has been shown to be maintained via a balance between selection and dispersal (Slatkin 1978, Endler 1980, Slatkin 1987, Phillips 1996, Kirkpatrick and Barton 1997). Likewise in studies involving more than one study environment a balance between divergent selection and gene flow has been suggested to maintain phenotypic variation (Gray and McKinnon 2007). The dispersal

of individuals may be affected by a number of different ecological and environmental conditions (Ims and Hjermann 2001), such as population structure, density or prevailing weather conditions. Furthermore, context-dependent dispersal may alter the gene flow between locally adapted populations and contribute to phenotypic variation within populations: migratory birds, for example, may have a prolonged migration journey, during which returning birds continue to areas beyond their former breeding grounds (Berthold 2001). This continued migration to higher latitudes has been suggested to be caused by environmental conditions along the migration route (Svärdson 1949, Kalela 1952).

1.1.3 Temporal variation in selection

Temporal changes in the phenotypic composition of a population may take place via phenotypic plasticity, micro-evolutionary change, gene flow or genetic drift. With regard to variation in heritable traits, temporally fluctuating selection acting on a quantitative trait can maintain genetic diversity within a population if the generations overlap (Ellner and Hairston 1994, Ellner 1996). The strength of selection has been shown to vary considerably in time (Siepielski et al. 2009, 2011): temporal variation in selection, for instance, has been reported to occur both within a single season (e.g. Qvarnström et al. 2000, Schmoll et al. 2005) and between seasons (e.g. Chaine and Lyon 2008, Lehtonen et al. 2010, Milner et al. 2010). Fluctuating selection on phenotypic traits has been found to play a role in maintaining phenotypic variation in several free-living populations (e.g. Chaine and Lyon 2008, Robinson et al. 2008, Punzalan et al. 2010, Morris et al. 2010). Overall, our understanding of the mechanisms behind temporal variation in the direction, strength and form of selection is still relatively poor, but variation in environmental conditions driven by climatic fluctuations seems to be both common and important (Siepielski et al. 2009).

1.2 Variation in bird colouration

Colouration in the animal kingdom is often strikingly variable. Animal colouration was of interest already to Darwin and Wallace, and has been widely studied since; it is inevitable to ask questions about the origin, control, function, evolution and variation in colouration. Colouration plays a major role in social associations such as sexual selection, and bright colouration and various adornments in animals are mostly assumed to have evolved through sexual selection (Darwin 1871, Andersson 1994, Hill 2006b). In birds, colouration has many functions. It is used in intraspecific signalling in a number of ways: to convey information as to quality, Fisherian attractiveness, behavioural strategies, genetic compatibility, kinship, individual identity and presence (Dale 2006). However, colouration may also act in several non-signalling functions, such as vision enhancement, protection from abrasion, bacterial degradation, or predation (Bortolotti 2006). In birds, colour polymorphism – inter-individual variation in colouration – is found in 3.5 % of species (Galeotti et al. 2003, Roulin 2004). The mechanisms maintaining polymorphism

are in many cases unclear, but in general colour polymorphism is suggested to have an adaptive function (Galeotti et al. 2003, Roulin 2004).

Colouration is produced either by different pigments or by structure. Different types of colouration differ in many ways, such as the extent of genetic control, their responses to hormones and their signalling effectiveness in different environments (Hill and McGraw 2006). Studies of the evolution and function of animal colouration have been dominated by variation in colouration with an environmental component; much less attention has been devoted to heritable colour variation (Roulin 2004). The most common form of pigmentation in birds is that caused by melanins, which yield various black, brown, grey and rufous colours. There are two categories of melanin pigments: eumelanin, conferring dark black or brown hues, and phaeomelanin, conferring reddish-brown hues (McGraw 2006). Melanins are endogenously produced, and their formation and deposition are known to be genetically controlled (McGraw 2006). However, there are also indications that the degree of melanism may be affected by environmental conditions (e.g. Griffith et al. 1999, Horth 2006, McGraw 2007, Roulin et al. 2008a, Lepetz et al. 2009), and that melanin colouration can be physiologically and energetically costly (Jawor and Breitwisch 2003, Griffith et al. 2006). Overall the sign and magnitude of selection on melanin colouration differs between species in birds (Meunier et al. 2011), and it often seems to depend on ecological (Antoniazza et al. 2010; Roulin et al. 2011) or environmental factors (Roulin et al. 2008b). Interestingly, variation in the degree of melanin-based colouration is often correlated with morphology, physiology, reproductive traits, or behaviour (Roulin 2004). These associations seem to be caused by the pleiotropic effects of the genes regulating the synthesis of melanin colouration (Ducrest et al. 2008). It has been suggested that melanin colouration may signal alternative adaptive strategies to particular environmental conditions (Roulin 2004, Roulin et al. 2008a, Roulin et al. 2008b, Piault et al. 2009). Melanin colouration may also play a significant role for example in thermoregulation (Roulin 2004, McGraw 2006), in feather structure (Bonser 1995, but see Butler and Johnson 2004), in microbial resistance (Burtt and Ichida 2004, Goldstein et al. 2004) and in protection from wear (Ward et al. 2002, Delhey et al. 2010). In addition to colours produced by pigments in the tissue, non-pigmented feathers in combination with pigmented ones also form striking plumage patterns, such as bars, spots and different patches that vary for example in size or frequency. Varying pigmented or non-pigmented patches are often considered to be ornaments, used in sexual selection (Andersson 1994). Depending on the case, the expression of ornamental patches may be affected by genes, condition of an individual, environment or parental effects (e.g. Gustafsson et al. 1995, Potti and Canal 2011).

In addition to colours produced by pigments, structural colouration at near-ultraviolet wavelengths (UV-A; 320–400 nm) is visible to birds (Cuthill et al. 2000). This colouration is produced by light interacting physically with nanometer-scale variation in the structure of an integument. In bird feathers, structural colours are produced by the coherent scattering of light waves from microscopic keratin structures within the feather barbs and barbules (Prum et al. 1999, Prum et al. 2003, Prum 2006). There is some

evidence that UV reflectance in bird feathers is heritable (Johnsen et al. 2003, Py et al. 2006), but there have also been several studies that have found condition-dependence (Keyser and Hill 1999, reviewed by Hill 2006a). In this thesis, I focus on variation in melanin-based and structural colouration and on non-pigmented ornamental patches in the plumage of pied flycatcher males.

1.3 The pied flycatcher as a model species

The pied flycatcher is a small, hole-nesting passerine that has been studied widely as a model species in numerous ecological and evolutionary studies during the whole of the 20th century (reviewed by Lundberg and Alatalo 1992, Sætre and Sæther 2010). Such a strong background enables biologists today to resolve many complex questions that would be out of reach without the former army of colleagues working with the species. There are several advantages to using the pied flycatcher as a study species: for instance, it accepts nest-boxes for breeding and tolerates the disturbance caused by researchers' repeated visits, captures and manipulations. The pied flycatcher is also common across most of its breeding range (Cramp and Perrins 1993), including Finland (Väisänen et al. 1998, Valkama et al. 2011). From the point of view of evolutionary biology, the most attractive character of the species is the wide variation in the male phenotype. During the breeding season the species is sexually dimorphic in plumage colouration: the females are all relatively alike, but the males differ in several secondary sexual characteristics, most of which have been shown to be sexually selected (see below).

The pied flycatcher breeds from Europe to western Siberia (Fig. 1) and winters in sub-Saharan Africa. The closely related semi-collared flycatcher (*Ficedula semitorquata*), which breeds in southeastern Europe, and the atlas flycatcher (*Ficedula speculigera*), which occurs in northern Africa, have earlier been described as subspecies of the pied flycatcher (Sætre et al. 2001b). The breeding range of the pied flycatcher does not overlap with these two species, while the distributions of the pied flycatcher and the closely related collared flycatcher (*Ficedula albicollis*) overlap in Central and Eastern Europe (Røskaft et al. 1986b, Lundberg and Alatalo 1992, Sætre et al. 1997, Sætre et al. 1999, Fig. 1). The pair of species diverged in allopatry during the Pleistocene glaciations (ca 2–0.1 mya) (the collared flycatcher in the Balkan area and the pied flycatcher in Iberian Peninsula), and have since then come into secondary contact in Central and Eastern Europe (Haffer 1989, Sætre et al. 2001a, Newton 2003). There is evidence of character displacement in the pied flycatcher in the sympatric area with respect to ecological, social and sexual traits (reviewed by Qvarnström et al. 2010, Sætre and Sæther 2010).

The melanin-based dorsal colouration (head and back) of pied flycatcher males varies from female-like brown to completely black (Drost 1936, Lundberg and Alatalo 1992), and is highly heritable (reported h^2 values varying from 0.6 to 0.88) (see Alatalo et al. 1994, Lehtonen et al. 2009a). Old males tend to be darker than young ones: a modest (ca 20 %, i.e. one Drost score) change occurs between the ages of one and two years

(Lundberg and Alatalo 1992). Collared flycatcher males are always black on dorsal side, whereas in areas of sympatry pied flycatcher males are mostly brown – probably due to avoidance of hybridization and interspecific competition with the collared flycatcher (e.g. Røskaft et al. 1986b, Král et al. 1988, Lundberg and Alatalo 1992, Sætre et al. 1997, Sætre and Sæther 2010). In allopatric areas both colour types occur, but with increasing distance from the Central European breeding areas the frequency of darker males – and thus also the level of sexual dichromatism – seems to increase (von Haartman 1949, Røskaft et al. 1986b, Lundberg and Alatalo 1992, Røskaft and Järvi 1992, Huhta and Siikamäki 1997, Haavie et al. 2000, Lehtonen et al. 2009a); this has often been assumed to be due to sexual selection for conspicuous colouration. In a sympatric population, pied flycatcher females were found to prefer brown males over black ones, while in an allopatric population they preferred mainly dark males (Sætre et al. 1997). It has been shown that the brown male colour type is beneficial for pied flycatchers in sympatric areas because it reduces harmful social/agonistic interactions (Slagsvold & Sætre 1991, Alatalo et al. 1994) and hybridisation (Sætre et al. 1997) with the socially dominant collared flycatcher (reviewed by Qvarnström et al. 2010, Sætre & Saether 2010). The role of the varying dorsal colouration of male pied flycatchers in allopatric areas has been studied extensively, but numerous studies have found no clear advantage for black males in mating or breeding success (see summary in chapter **II**, Appendix 1).

The ultraviolet (UV) reflectance of the plumage is sexually selected in the pied flycatcher at least in an allopatric area in Finland (Siitari et al. 2002, Lehtonen et al. 2009b), but possible spatial variation in the trait and in selection on it remain unknown. In addition to melanin-based and structural colouration, pied flycatcher males display conspicuous white ornamental patches that vary greatly in size and shape. Most males have a white forehead patch, the size of which has a heritable component but is also affected by environmental and parental effects (Potti and Canal 2011, but see Dale et al. 1999). The trait is sexually selected at least in a Spanish population (Potti and Montalvo 1991, but see Galvan and Moreno 2009). In other studies the forehead patch size has not been found to be a mating advantage (Dale et al. 1999, Galvan and Moreno 2009), or to affect the probability of siring extrapair young (Lehtonen et al. 2009b). In addition to the forehead patch males have large white wing patches, formed mostly by white areas in the tertial feathers. Most males also bear white areas in the outer tail feathers (hereafter called tail patches) that vary in size and shape. The importance of the wing or tail patch has been studied relatively little compared to the forehead patch size, and to my knowledge no studies of selection acting on these traits have thus far been reported.

Overall, male plumage traits are known to be inter-correlated (e.g. Dale et al. 1999, Siitari and Huhta 2002, Belskii 2006, Menchinsky 2006, Ivankina et al. 2007). In addition to plumage characteristics, selection may also act on other male traits that are correlated with plumage colouration. Male song characteristics have been shown to be important in mate choice (Lampe and Espmark 2003), and correlate with male plumage traits (Lampe and Sætre 1995). Likewise male behavioural traits, such as singing activity (Ilyina and Ivankina 2001), have been shown to be associated context-dependently with plumage

characteristics. In addition, male age has been suggested to be important in female mate choice, but it is not clear whether females gain any advantage by choosing old males over young ones (Alatalo et al. 1986a, Sætre et al. 1995).

1.4 Aims of the thesis

The aim of my thesis is to take a step towards a better understanding of the mechanisms that maintain phenotypic variation in natural populations. Using the pied flycatcher as a model species, I study spatial and temporal variation in phenotypic traits and the selection pressures acting on plumage colouration, with large data sets and with manipulative experiments conducted in the field.

The first two articles deal with spatial variation in the male colour phenotype and selection on it in the breeding range of the pied flycatcher. I first describe patterns of phenotypic variation in several correlated plumage traits (**I**). In addition, the variation in plumage traits in the pied flycatcher males is compared to plumage colouration in the sister species, the collared flycatcher; I test the possibility that the among-population variation is explained by character displacement with the sister species (**I**). Next, I examine selection acting on multiple plumage traits among breeding populations (**II**). Selection estimates from different populations are further used to determine the presence of consistent selection patterns among populations, and whether selection is associated with the geographical location of the population or with the average plumage traits observed (**II**). I also investigate the relationship between the different fitness components and the role of indirect selection on them, across the breeding range of the pied flycatcher (**II**).

In **III** I investigate the possibility that different male phenotypes are adapted to breed in different environmental conditions. Using long-term data, I investigate selection acting on plumage traits by examining the relative breeding success of different male phenotypes under different weather conditions (**III**). **IV** deals with temporal variation in the proportions of different male phenotypes in the study population. By determining the causes of yearly variation in the phenotypic composition of a population, I hope to uncover the factors that may cause long-term shifts in the phenotypic composition of a population (**IV**).

In order to understand the role of sexual selection acting on plumage traits in more detail, I experimentally distinguish between territory-related resources and male quality: do females choose for male traits or for territory quality? And which male traits are associated with success in female mate choice? (**V**). In addition, I manipulate male UV colouration to test the causal role of the trait in mate choice.

2. MATERIALS AND METHODS

2.1 Study species

The study species in this thesis is the pied flycatcher. In addition, in the description of spatial variation in male plumage traits (**I**), comparisons are drawn between the pied and the collared flycatcher. These closely related insectivorous species are relatively similar in their ecology. Both species breed in Europe (Fig. 1) and winter in sub-Saharan Africa, the pied flycatcher on average in more western areas and the collared flycatcher in more eastern ones. In the pied flycatcher the mean clutch size is six, the incubation period is 13–15 days, and the nestling period is 14–16 days (Lundberg and Alatalo 1992, Cramp & Perrins 1993).

The pied flycatcher shows high breeding site fidelity (e.g. von Haartman 1949, Creutz 1955, Lundberg and Alatalo 1992), but natal site fidelity is mostly low. The return rates of nestlings vary between geographical areas, from about 14 % in England and northern Germany to less than 2.4 % in the northern and eastern populations (Lundberg and Alatalo 1992, Lehtonen et al. 2009a). Most of the natal dispersal distances observed are short (Lundberg and Alatalo 1992) but distances of hundreds of kilometres have also been reported (Glutz von Blotzheim and Bauer 1993, Vysotsky 1994).

2.2 Study areas

The data on spatial variation in phenotypic traits and in selection pressure acting on phenotype have been collected at several study sites across the breeding range of the pied flycatcher (Fig. 1) (**I**, **II**). With the help of a wide network of collaborators, a standardised data set on plumage colouration and selection on it was collected from 20 populations across the breeding range.

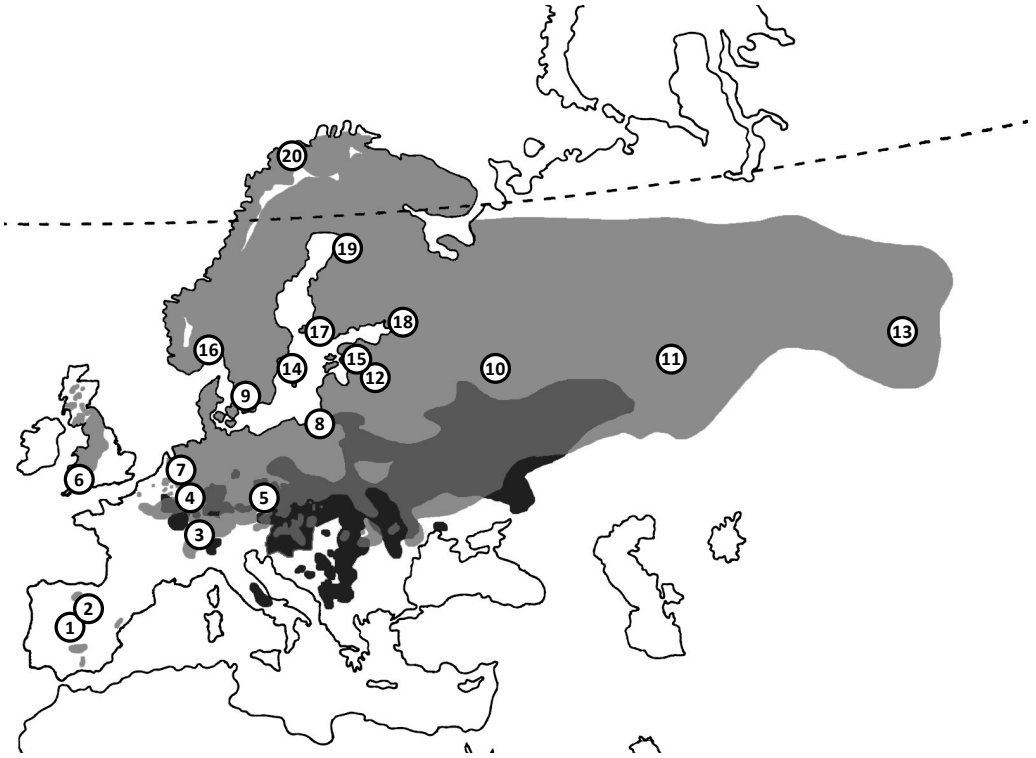

Figure 1. Populations sampled in studies of geographical variation among populations (**I**, **II**). Light grey represents the breeding range of the pied flycatcher alone, medium grey the sympatric breeding area of both the pied and the collared flycatcher, dark grey the breeding area of the collared flycatcher alone. White circles indicate locations of study populations: Valsaín-Lozoya, Spain (1); La Hiruela, Spain (2); Vaud, Switzerland (3); Harthausen, Germany (4); Moravia and Jeseníky mountains, Czech Republic (5); East Dartmoor, United Kingdom (6); Drenthe, Netherlands (7); Courish spit, Russia (8); Vombs fure, Sweden (9); Moscow region, Russia (10); Central Urals, Russia (11); Kraslava, Latvia (12); Tomsk, Russia (13); Gotland, Sweden (14); Kilingi-Nõmme, Estonia (15); Oslo, Norway (16); Ruissalo, Finland (17); Karelia, Russia (18); Oulu, Finland (19); Skibotn, Norway (20). The map is based on *Birds of the Western Palearctic* (Cramp and Simmons 2006) and on Flint et al. (1984) modified according to information gained from co-authors.

The long-term data set used in **III** and **IV** were collected in the Kimpari study area (60°15'N, 24°18'E), located in the Siuntio municipality, southern Finland, about 30 km from Helsinki (Fig. 2) during 1982–2008. The study area consisted of two study plots about 300 m apart and contained altogether 160 nest boxes (see further Virolainen 1984). The study area is located in the northern range of the hemiboreal zone, and is mostly covered by coniferous forest with a mixture of deciduous trees. The study area was established by the Kimpari Bird Projects (KBP), a group of enthusiastic amateur ornithologists. Martti Virolainen, one of the members of the KBP, has been intensively monitoring pied flycatchers in the Kimpari area from the late 1960s to the present.

The other long-term data used in **IV** were collected in the study area of Askainen in southwestern Finland (60° 30' N, 21° 45' E) (Fig. 2) during 1954−1994. The number of nest boxes in the area varied between 79 and 155. The study area is located in the northern range of the hemiboreal zone, and contains a mixture of deciduous, mixed and coniferous forest. The area was monitored from the 1940s to the 1990s by professor Lars von Haartman, whose main scientific life-work concerned the pied flycatcher.

Field experiments (**V**) were carried out on Ruissalo Island (60°25'N, 22°7'E) in the city of Turku in southwestern Finland (Fig. 2). The area is located in the northern range of the hemiboreal zone. One part of the study area consists of 111 nest boxes, located around the Botanical Gardens of the University of Turku and in the nearby oak forests. The other part of the Ruissalo study area consists of ten separate woodlands, further divided into territory sites (see below). The habitat in the second part of the study area is variable, consisting of mixed and coniferous forest.

Figure 2. Study populations in southern Finland (**III**, **IV**, **V**). White circles indicate locations of study populations: Askainen (A), Ruissalo (R) and Kimpari (K).

2.3 Male traits measured

Parent birds were captured during the breeding period and ringed with aluminium rings. The birds were aged as young (1 yr) or old (> 1 yr) on the basis of several aspects of feather wear (**I**, **II**, **III**, **IV**, **V**) (Karlsson et al. 1986, Lundberg and Alatalo 1992, Svensson 1992). The morphological traits measured were wing length (mm), tarsus length (mm) and body mass (g) (**V**). In order to monitor breeding success, nest boxes were checked at least once a week to determine the laying date of the first egg, clutch size, and the number of nestlings, fledglings and dead nestlings (**II**, **III**, **IV**). The laying date was determined from the number of eggs observed during egg laying,

assuming a laying frequency of one egg per day (Creutz 1955, Lundberg and Alatalo 1992).

The dorsal eumelanin colouration on the head and back of males was estimated in the field either by Drost scores (Drost 1936) or by blackness percentages, from 0 % to 100 % (**I**, **II**, **III**, **IV**, **V**). Drost scores I and II represent black males, but in group I the rump is black while in group II it is lighter. Groups III–VI are intermediate, and in group VII males are completely brown in their dorsal colouration (for a detailed description, see Drost 1936, Lundberg and Alatalo 1992, Glutz von Blotzheim and Bauer 1993).

The second tertial feathers (of a total of three tertial feathers per wing) were collected for UV reflectance measurements (**I**, **II**, **V**). I decided to measure UV reflectance from the tertial feather because white feathers typically have higher UV reflectances than dark ones (Eaton and Lanyon 2003), and because the tertials have a rigid feather structure, unlike the soft plumaceous structure of dark or brown body feathers. The UV reflectance of the white part of the feather was measured in the laboratory with a spectrophotometer. Measurements were taken perpendicularly to the feather surface. To measure reflectance in the ultraviolet part of the spectrum, I calculated the proportion of ultraviolet light out of overall reflectance (relative UV reflectance or UV chroma; $R_{320–400\ nm} / R_{320–700\ nm}$). A mean of three measurements per feather was used in the analyses.

The forehead, wing and tail patches were photographed in the field with a digital camera (**I**, **II**, **V**). In each picture, a ruler or other scale was held at the same distance from the camera as the target ornamental patch. The sizes of the white areas were measured from the photographs with ImageJ software (Abramoff et al. 2004). The forehead patch was photographed directly from the front (Fig. 3), the wing patch when the wing was in resting position (Fig. 3). If the forehead patch consisted of two separate patches, the area of the separate parts was summed and the sum was used in the analyses. The tail feathers were photographed with the white areas in the outermost feathers on one side of the tail separate from each other (Fig. 3); thus the total area of white was visible. The tail patch area was calculated as a sum of these white areas. In the long-term study of the associations between male traits and breeding success (**III**), the forehead patch size was measured in the field with callipers. The wing patch size was not directly measured in the field; rather, the proportion of white in the second tertial feathers was estimated at 5 % intervals. The amount of white in the tertial was highly correlated with the area of the whole wing patch measured in a sample of birds, and I therefore applied the proportion of white in the second tertial as an estimate of wing patch size (**III**).

Figure 3. Some examples of males with different dorsal colouration, forehead, wing and tail patches photographed in southern Finland.

In addition to plumage traits, male song was also recorded (**V**). Of the males recorded, at least 25 song strophes per male were recorded during mornings before pairing. Song strophe length, the total number of syllables, the number of different syllables and finally the versatility index were derived from sonograms. The song versatility index was calculated by dividing the number of different syllables by the total number of syllables in a sample of 25 male song strophes.

2.4 Data on environmental conditions

Temperature (**III**, **IV**) and rainfall data (**III**) were used to indicate local environmental conditions. Mean values were calculated for different periods during the migration, arrival and breeding phases from the daily mean temperature (°C) and precipitation (mm). A cumulative thermal sum of mean daily temperatures exceeding 0 °C was used to indicate spring phenology. Finnish temperature and rainfall data were provided by the Finnish Meteorological Institute. The temperature data for locations outside Finland were obtained from the European Climate Assessment & Dataset project (Tank et al. 2002).

2.5 Experiments

In order to be able to distinguish between the relative importance of male characteristics and territory quality in mate choice, I experimentally randomised territory quality among arriving males following the design of Alatalo et al. (1986b) (**V**). The experiment was conducted in separate woods, located at a minimum distance of 300 m from each other. Within these woodlands, territory sites were chosen beforehand. As there are very few natural tree-holes in these areas, pied flycatchers breed almost exclusively in the nest boxes that are provided. At the beginning of the experiment, one site per woodland was drawn at random and the first pair of nest boxes was established in that territory site. The first male arriving in a woodland thus only found a single pair of nest boxes. As soon as the first random-drawn site was occupied by a singing male, another nest box pair was established at the second random-drawn territory site. Arriving males thus found only a single vacant pair of nest boxes, and had no opportunity to choose between territory sites within a woodland. After the males had settled, females were allowed to choose between males. After this the first females were removed and released at two locations more than 30 km away from the study area, while at the same time the UV reflectance of the males was manipulated (see below). A set of new females was then allowed to choose between the males. In the course of the experiment, the pairings of the males were monitored twice a day.

To assess the role of UV reflectance in mate choice in more detail, the relative UV reflectance of the males' head, back and wings was manipulated or control-treated. The reduction in the UV reflectance of the manipulated males was accomplished by applying a mixture of UV-absorbing chemicals and duck preen gland fat (Andersson and Amundsen 1997, Johnsen et al. 1998, Sheldon et al. 1999, Limbourg et al. 2004, Korsten et al. 2006, Korsten et al. 2007). The control males were treated only with the fat. The reduction in UV reflectance diminishes with time, but is known to last about a week (Korsten et al. 2007).

2.6 Data analyses

To investigate the acting of selection on different plumage traits among populations, I calculated standardised selection estimates (**II**). Selection was described in standardised terms, as only by this means is it possible to quantitatively compare selection in different populations (and across studies). For this purpose I used the approach developed by Lande and Arnold (1983) and Arnold and Wade (1984). In this method, linear regression models are used to calculate estimates of selection pressure (*selection differentials*). The dependent variable in these regressions is the standardised fitness measure (fitness divided by its mean value). The explanatory variables are various phenotypic traits, which are standardised to a mean zero and a variance of one. As selection often acts on several correlated traits simultaneously, the role of indirect selection may be important. Partial selection coefficients were calculated to control for the indirect effects of other traits. This was done by calculating partial selection differentials (*selection gradients*). The partial selection differentials were estimated by multiple linear regressions with a standardised fitness component as a dependent variable and standardised phenotypic traits as explanatory variables (Lande and Arnold 1983, Arnold and Wade 1984). The selection estimates were based on the benefits arising from early breeding (breeding date selection) and from a high number of fledglings (annual fecundity selection) by the most attractive males (Fisher 1930, Kirkpatrick et al. 1990, Møller et al. 2006a).

In addition to standardised selection estimates, selection was investigated by comparing the reproductive success of different male phenotypes in different environmental conditions (**III**). This was done by studying interactions between male phenotype and prevailing weather conditions on different components of breeding success (timing of breeding, clutch size, nestling survival and fledgling production). In investigating mate choice in greater detail, pairing success was measured by monitoring the time (in days) before pairing (**V**). To compare the pairing success of males from different parts of the study area, standardised rank values were calculated. Pairing success was also compared to male characteristics (**V**).

Model selection based on Akaike's Information Criteria (Burnham and Anderson 2002) was used to find out which of the hypotheses best explained our study questions (**IV**). The best models were selected based on Akaike's Information Criterion for small sample sizes (AICc) (Burnham and Anderson 2002, Johnson and Omland 2004), where the model with the lowest AICc value best fits the data.

3. MAIN RESULTS AND DISCUSSION

3.1 Spatial variation in male plumage traits across the breeding range (I)

There were significant differences among the pied flycatcher populations in all five studied male plumage traits. The different plumage traits were strongly or moderately inter-correlated, suggesting that the traits evolve at least to some extent together. In general, black males had higher UV reflectance than brown males, larger forehead and wing patches, and smaller tail patches.

In the sympatric area of the two species, the pied flycatcher differed strongly from the more conspicuous collared flycatcher in all the major visual male plumage traits. This result strengthens the earlier evidence for character displacement affecting plumage colouration in pied flycatcher males breeding in sympatry (reviewed by Qvarnström et al. 2010, Sætre and Sæther 2010). Overall conspicuousness was also found to increase with growing distance from the sympatric area. In particular, the mean dorsal colouration darkened and the mean forehead and wing patch sizes increased, while the tail patch size decreased gradually with distance from the collared flycatcher breeding range. Since all the major male plumage traits change in relation to distance from the breeding area of the collared flycatcher, the results provide evidence that the pied flycatcher has diverged from its sister species in the area of secondary contact simultaneously in all these plumage traits. Gradual variation in the phenotype is typically considered to be driven by local adaptations to an environmental gradient (Slatkin 1973, Kirkpatrick and Barton 1997). The current evidence provided by this study, however, indicates that a cline in the phenotype over a large geographic area may reflect a single selective force and local adaptation to the social environment in the sympatric area. The evolution of plumage colouration in allopatric populations has been suggested to be driven by sexual selection towards conspicuous colouration, but documented selection has been relatively weak and variable (see **II** and references therein). The gradual increase in conspicuousness with distance from the sympatric area is suggested to be driven by extensive gene flow (Lehtonen et al. 2009a) and context-dependent selection occurring in allopatric populations (**III**). Overall, the ongoing process of divergence in sympatry and potential convergence in allopatry offers an example of the evolution of highly divergent avian plumage patterns, which often include remarkable, rapidly evolved differences between closely related species (Martin et al. 2010). In the case of geographical variation in the pied flycatcher male plumage colouration, however, the roles played by several factors, such as temperature, humidity, predation pressure and their temporal variation, remain unknown.

3.2 Spatial variation in selection on multiple plumage traits across the breeding range (II)

I show that selection on different male plumage traits varies among populations. Examination of the relationships between different fitness components showed that the selection on male dorsal colouration was divergent between breeding date and fecundity selection. Roughly half of the populations showed consistent selection for dark colouration, while the other half differed in the direction of selection between breeding time and number of offspring produced. Similar divergent selection pressures between life-history stages have been reported for several species (Møller 1989, Grant 1990, Roff 1992, Robinson et al. 2006). Divergent selection has also been suggested to be relatively common in nature and to lead to evolutionary trade-offs, which can constrain the response to selection (Schluter et al. 1991, Roff 1997). The results thus suggest that variation in male melanin-based dorsal colouration within populations may partly be maintained by conflicting selection between life-history traits.

Selection acting on male tail patch size was associated with distance from the sympatric area with the closely related collared flycatcher. Birds breeding close to the sympatric area typically showed selection for larger tail patch size, while further away selection was weak or occurred in the opposite direction. This is to my knowledge the first report that selection acts on tail patch size in the pied flycatcher, and that it furthermore differs between populations. In addition, selection was associated with the mean observed expression of the trait among populations: selection for large male tail patch size occurred in populations with a large mean patch size, and vice versa. In the sympatric area a large male tail patch can be expected to be an advantage in species recognition and in avoiding social conflicts with the sister species (see Qvarnström et al. 2010), whose males have small tail patches. Interestingly, unlike other male plumage traits the tail patch can be hidden or exposed by altering the position of the tail feathers. The results suggest that selection for large tail patch size is caused by inter-specific interactions and is reflected to the surrounding allopatric area via gene flow, which has been shown to be considerable (Lehtonen et al. 2009a). However, tail patch size may also reflect adaptation to other conditions than intraspesific relationships with collared flycatcher. On the other hand, when ornament size is not constricted by interspecific selection, it may be used as a mate choice cue. Ornamental patches are often suggested to indicate male quality (Andersson 1994), and may be condition-dependent. Since the size of other ornamental patches (wing and forehead patch) in pied flycatcher males is expected to be counterselected due to interspecific competition, the role of the tail patch size may be important in sexual selection in the sympatric area and its proximity. Other questions – the role of tail patch size in sexual selection, the age-dependence of the trait, its possible variation among populations, and the factors affecting spatial variation in selection acting on the trait – remain to be investigated in future studies.

Interestingly, current selection on other traits than tail patch size were not associated with the observed mean plumage traits among populations, although spatial phenotypic

variation is often suggested to have formed due to underlying selection (Slatkin 1973). Similarly my results indicate that, regimes of sexual selection in particular vary in a relatively fine-grained way, even if the phenotype shows a cline (Svensson and Sinervo 2004, Gosden and Svensson 2008). Differences in selection on male plumage traits between populations located in close proximity have also been reported earlier for the pied flycatcher (Galvan and Moreno 2009, see summary in Appendix 1). In general, spatial and temporal selection mosaics have been predicted to be the rule rather than the exception (Cornwallis and Uller 2010). The factors causing spatially variable selection, however, often remain unknown. The present results suggest that studies dealing with intraspecific interactions or environmental conditions may provide a better understanding of shifting selection pressures.

3.3 Temperature-dependent variation in selection (III)

The comparison of the relative breeding success of different males under different environmental conditions revealed that the effects of weather conditions on the relative breeding success of different male phenotypes varied between different phases of breeding. The reproductive output of black males was highest if it was first relatively cold during egg-laying and then warm during the nestling period. In contrast, brown males succeeded best when it was warm during the whole breeding season. The large clutch size of females paired with black males during cold weather may be related to direct or indirect benefits for the female. Differences in activity between brown and black males in cold weather (Ilyina and Ivankina 2001) may be directly reflected in courtship feeding frequency and female condition. Alternatively, females may allocate resources depending on the quality of a male (Sheldon 2000), and may invest more in the clutch when paired with an active black male during a cold spring. In contrast to the egg-laying period, I found that the nestlings of black males suffered more from nestling mortality during cold weather than the nestlings of brown males. The difference may be related either to the temperature-dependence of parental care in black males or to the sensitivity of the offspring of black males to cold temperatures. The temperature sensitivity of the nestlings seems to be a more probable explanation, since black males have been reported to be actually more active at low temperatures than brown ones (Ilyina and Ivankina 2001). Both the degree of melanin colouration and the regulation of energy homeostasis are known to be pleiotropically affected by the melanocortin system (Ducrest et al. 2008). Black males have a higher basal metabolic rate than brown ones (Røskaft et al. 1986a, Kerimov et al. 2006), and the rate is known to be heritable (Bushuev 2009, Bushuev et al. 2011). It is possible that in cold temperatures the nestlings of black males have higher energy demands, which cannot be satisfied by the parents when insect abundance is low. The results suggest that males with a high degree of melanism may be adapted to seasonal climates where temperatures are low in spring but rise steeply towards summer. In contrast, the brown males may be best adapted to breed in environments that are warmer during the whole breeding season. Thus different phenotypes may represent different strategies, adapted to different conditions (Roulin 2004, Roulin et al. 2008b).

Overall, fluctuating selection may maintain variation both in heritable black-brown colouration and in other male traits that are genetically correlated with it.

My results indicate that male forehead and wing patch sizes have context-dependent effects on the timing of breeding and nestling mortality, respectively. In the pied flycatcher, early breeding is beneficial as the clutch size and recruitment of offspring typically decreases with the progress of the breeding season (Lundberg and Alatalo 1992). In cold weather conditions, males with large forehead patches started breeding earlier than those with small patches. This earlier breeding of males with large forehead patches in cold spring may be related to context-dependent success in intra-sexual competition, to female mate choice, or to a combination of both selection mechanisms. Intra-sexual competition may lead to differences in the amount of resources available for reproduction, if males with large forehead patches are able to occupy the best territories with the best food supplies despite the cold weather. Females may directly choose good quality territories, or males with large forehead patches may acquire benefits from food resources that are important for mating success. On the other hand, low temperatures can raise the costs of egg-production (Salvante et al. 2007). Thus the benefits of for example high-quality territory for a female may be temperature-dependent, so that good territory resources play a significant role only under cold weather conditions. During rainy nestling periods, the nestlings of males with large wing patches suffered less from nestling mortality than those of males with small patches. High rainfall is known to negatively affect nestling growth (Sanz 1995) and fledgling success (Eeva et al. 2002), possibly by reducing the availability of insect food. The results of this thesis suggest that males with large wing patches may succeed in feeding their young more efficiently than those with small ones despite rainy weather conditions. This study provides a starting point for understanding the context-dependent nature of selection on both forehead and wing patches; there is a clear need to study the condition-dependence of these ornaments as well.

3.4 Factors affecting temporal variation in the phenotypic composition of a population (IV)

Heritable phenotypic traits can provide visible proxies for changes in the genetic composition of populations (e.g. Karell et al. 2011). I show that the proportion of the brown pied flycatcher male phenotype has decreased in southern Finland over the last sixty years, from roughly one third to one sixth of breeding birds. Similar rapid phenotypic changes within a population have only rarely been documented (Zink and Remsen 1986). In the tawny owl (*Strix aluco*), the frequency of different colour phenotypes has changed during the last 48 years in Finland due to altered winter conditions (Karell et al. 2011). In the barn owl (*Tyto alba*), directional selection on females have been shown to cause an increase in melanic spot diameter in just 12 years (Roulin et al. 2010). In the black-tailed godwit (*Limosa limosa*), male ornamentation has decreased over a period of 160 years,

potentially due to changes in selection pressure caused by human-induced changes in breeding and non-breeding habitats (Schroeder et al. 2009).

While the proportion of brown males breeding in southern Finland has decreased during the study period, the proportion has varied considerably from year to year. I found that the relative breeding success of brown males in the previous two breeding seasons was associated with the proportion of brown males observed in the study area. The relative breeding success of brown and black males is dependent on the prevailing weather conditions (**III**); these findings strengthen the idea that environmental perturbations play a key role in maintaining phenotypic diversity in the pied flycatcher. Although it has been shown that the highly heritable male colouration in pied flycatchers can change due to fecundity selection under changing climatic conditions (**III**), the declining trend in the proportion of brown males seems nevertheless not to be driven by altered selection at the breeding grounds. Fecundity selection on the plumage colouration of pied flycatcher males fluctuates at short intervals (in terms of single years), but mean selection over longer periods has apparently not changed. The same pattern has been observed in several other free-living species (Kinnison and Hendry 2001, Hairston et al. 2005).

The results of this thesis suggest that the immigration of brown phenotype males from the Central European population also seems to contribute to the maintenance of variation in the colouration of male pied flycatchers, and immigration in turn seems to be affected by environmental conditions. I found that when the weather in northern Central Europe during the birds' migration was relatively warm, the proportion of breeding brown males in southern Finland was high, indicating that there is context-dependent immigration from Central European populations with mainly brown males. Dispersal is known to be affected by several environmental factors (Ims and Hjermann 2001, Bowler and Benton 2005), and recently it has been reported that changing temperatures may be associated with changes in dispersal (Møller et al. 2006b, Massot et al. 2008). The present results support earlier suggestions that birds may prolong their migration if migration conditions are good (Svärdson 1949, Kalela 1952). In general, the results also support the idea that species are able to adjust their breeding to climate change by prolonged migration to higher latitudes, as suggested earlier (Coppack and Both 2002).

Although immigration seems to affect phenotypic variation in the study population, I found that the effect of spring temperatures on the proportion of brown males observed in the study area has decreased from the 1950s to the present. The pied flycatcher population in Central Europe has declined more than the one in northern Europe (Glutz von Blotzheim and Bauer 1993, Hagemeijer and Blair 1997, Both et al. 2010) and the decline seems to be linked to climate change (Both et al. 2006, Both et al. 2009, Both et al. 2010). I suggest that as a consequence of this population decline, the immigration potential from areas dominated by brown males to higher latitudes has likewise declined during the last decades. The decline in immigration potential in turn is presumably causing the vanishing of the effect of spring temperatures on the proportion of brown males. The change in immigration potential may thus explain the decrease in the proportion of the

brown male phenotype from the 1950s to the present. Altogether this study provides an example how different environment-dependent mechanisms can simultaneously affect the phenotypic composition of a population.

3.5 Mate choice (V)

To be able to understand sexual selection, it is important to distinguish among the mechanisms underlying mating success. I show that when males are not allowed to choose between different territories before pairing, the females choose multiple male traits. When territory quality was randomised among arriving males, females were attracted by high UV reflectance, large wing patch, large morphological size and versatile song. These favoured male traits develop in different life stages, and may signal different aspects for females. Size being largely heritable (e.g. Merilä 1997), females may choose indirect benefits to their male offspring, such as good competitive ability via large size (e.g. Bolund et al. 2007). Size (e.g. Merilä 1996, Dubiec et al. 2006) and possibly song versatility may reflect the developmental conditions of a male, which may in turn signal other components of quality that are affected by early growing conditions. In addition, the complexity of the song may signal experience (Espmark and Lampe 1993) or the male's ability to learn songs, which may be heritable (Airey et al. 2000), possibly indicating genetic quality. Both the size and the structural UV colouration of the wing patch were selected, showing that even the same ornamental trait can include several signal components, and suggesting that the wing patch may be considered a multicomponent trait. Wing patch size and its UV reflectance are suggested to reflect the environmental conditions during moult at the wintering grounds, where the species is territorial and individuals do not have equal access to resources (Salewski et al. 2002), but the possible heritability and condition-dependence of these traits remain mainly unknown. Similarly, several components of a composite trait have been documented to be simultaneously favoured by females (e.g. Basolo and Trainor 2002, Calkins and Burley 2003, Trainor and Basolo 2006), and females may gain different information from different components. In general, mate choice in the pied flycatcher is complex, involving many different signal components, as also seems to be the case in several other species (Jennions and Petrie 1997, Candolin 2003). For example, different signals may play a role at different distances: plumage traits at a short distance but song at a greater one (e.g. Lampe and Espmark 2003). It remains to be studied whether different signals also have different values for different females. In general, multiple signalling has been suggested to arise from dynamic variation in selection pressures driven by environmental fluctuations (Bro-Jørgensen 2010). Studying the roles of different traits in different contexts may prove a fruitful research approach toward understanding the use of multiple ornaments in sexual selection in the pied flycatcher.

Experimental data showed that female preference for male UV reflectance is context-dependent. First, the importance of the UV reflectance of the wing patch for female preference depended on the background, in this case the dorsal black-brown colouration.

UV reflectance had a greater effect on pairing success in black males than in brown ones. The results suggest that in addition to differences in colours, the relationships among colours may also be important in signalling, and that the role of contrasts should be considered in studies of sexual selection (see Endler and Mielke 2005). Secondly, female preference depended on the time within the pairing season: early in the season females chose males with high UV reflectance, while later in the season the trait seems to be unimportant. The breeding season for the pied flycatcher is very short (Lundberg and Alatalo 1992), and the time for mate choice is restricted (Alatalo et al. 1988, Slagsvold et al. 1988). If the cost in relation to the time of prospecting for males is growing compared to variation in the quality of possible candidates, female choosiness is expected to decrease with time (Gibson and Langen 1996). It is thus possible that females are choosier early in the season, as the benefits of finding a good quality male are higher compared to the time constraint. This finding of time-dependence in female mate choice adds to a growing number of studies showing that female mate choice is context-dependent (e.g. Alonzo and Sinervo 2001, Qvarnström 2001, Oh and Badyaev 2006, Royle et al. 2008). These results underline the importance in studying mate choice cues of looking at entire patterns of traits rather than separate, individual traits. Overall, the thesis foregrounds the complexity of mate choice, which is shown to be dependent on multiple male traits and temporally plastic. Mate choice in the pied flycatcher is affected both by mate characteristics and by nest site quality (see also e.g. Alatalo et al. 1986b, Lifjeld and Slagsvold 1988). However, we still lack studies of the costs and benefits of preferred traits, which would enable us to draw conclusions as to the evolution of male traits and female preferences.

4. CONCLUSIONS AND FUTURE PROSPECTS

The main conclusion of this thesis is that there are several mechanisms contributing to the maintenance of phenotypic variation in male plumage colouration in the pied flycatcher. I found wide variation in all the studied male plumage traits among populations (**I**). The gradients in plumage colouration in relation to the sympatric area with the collared flycatcher seem to reflect the selective force related to interspecific interactions and further gene flow among populations (**I**). I show that selection on plumage traits is variable among populations, and thus apparently serves to maintain phenotypic differences between populations (**II**). The results based on long-term data support the general idea that environmental heterogeneity plays an important role in maintaining phenotypic variation (**III**, **IV**). In relation to environmental heterogeneity, I first show that selection within a population is dependent on the interactions between male phenotype and prevailing weather conditions (**III**). The proportions of different phenotypes in a population are furthermore shown to vary in response to fluctuating mean selection and to immigration, which in turn is suggested to depend on weather conditions during migration (**IV**). Overall, the results suggest that divergent selection between life-history traits seems to contribute to the maintenance of variation in melanin-based dorsal colouration (**II**, **III**). In addition, the findings suggest that context-dependent mate choice (**V**) and selection acting simultaneously on several correlated traits (**II**, **V**) contribute to the persistence of phenotypic variation within a population.

The use of multiple signals seems to be common in birds (Dale 2006). In the pied flycatcher, female preference seems to depend on multiple mate choice cues (**V**), and selection acts simultaneously on several correlated male plumage traits (**II**). The use of multiple traits in mate choice may reduce the variance in mating success among males and thus maintain variation in male traits within a population (Candolin 2003). The correlations between plumage colouration and indirect selection acting on the traits suggest that plumage traits evolve as a group (**I**, **II**, **V**), indicating a need to investigate more deeply the role of relationships between phenotypic traits. As often in the field of ecology, the results emphasise the importance of studying complete trait patterns and multiple contexts, rather than comparing one or a few aspects at a time.

Overall, there is a growing number of studies showing that both natural and sexual selection on phenotype is dependent on a variety of ecological and environmental factors (e.g. Qvarnström 2001, Grant and Grant 2002, Garant et al. 2007, Chaine and Lyon 2008, Robinson et al. 2008, Narraway et al. 2010). In the pied flycatcher, selection acting on male dorsal black-brown colouration and on forehead and wing patch sizes seems to be dependent on environmental conditions (**III**). In addition, female mate preference for UV reflectance is context-dependent with respect to other male characteristics and to the time within a pairing season (**V**). Context-dependent mate choice is assumed to maintain phenotypic variation, but the possible adaptive mechanisms still remain unclear.

Context-dependent plasticity in mate choice preference can be adaptive if the benefits are direct, i.e. occurring simultaneously in the prevailing conditions; or, in the case of indirect benefits for offspring, if there are cues available as to the conditions that the offspring will encounter (Qvarnström 2001, Kokko and Heubel 2008). The findings of this thesis show that in the pied flycatcher context-dependent selection on male plumage colouration traits differs between different breeding periods (**III**), while selection on dorsal colouration diverges between different phases of breeding in several populations (**II**). The results encourage a deeper investigation of the role of environment-dependent mate choice together with variation in environmental conditions within and between seasons.

The decline in the proportion of the brown phenotype in the pied flycatcher population (**IV**) reflects a loss in genetic diversity within a population. Such an effect may weaken the potential for future adaptive responses (Frankham et al. 2002). In general, polymorphic populations are on average predicted to be less vulnerable to environmental change and at lower risk for range contractions and extinctions compared to species with a non-variable phenotype (e.g. Forsman et al. 2008, Forsman and Hagman 2009, Roulin et al. 2011). In this thesis I hope to have shed more light on the evolutionary processes that will influence future biodiversity, since an understanding of these processes is essential at a time of rapid human disturbances (Hendry et al. 2010). One of the broader implications of my findings is that the current process of climate change has a strong potential to rapidly alter the phenotypic composition of populations. Predicting the consequences of climate change and other environmental changes may be highly complex, as net selection may depend on genotype-by-environment interactions between different life-history stages.

In the experimental parts of the thesis I hope to have drawn attention to the importance of distinguishing between mate and resource qualities in mate choice. The combination of experimental methods (randomising territorial quality and trait manipulation) that I have used has the potential to be applied to other free-living species. However, we still lack manipulatory studies dealing with resource quality, density of suitable breeding sites, or multiple mate characteristics simultaneously; such studies would shed more light on the complicated process of sexual selection.

In order to deepen our understanding of phenotypic selection in free-living populations, spatial and temporal aspects of selection should be integrated in future studies. In the pied flycatcher this seems to be an attainable goal, enabled by the active collaboration network. In general, several possible factors that may contribute to the persistence of phenotypic variation in pied flycatcher male colouration remain to be studied. First of all, we still lack information on the possible costs, condition-dependence and heritability of several phenotypic traits, which restricts the conclusions that can be drawn as to the maintenance of phenotypic variation. In future studies, the role of immigration potential between phenotypically differing populations should be examined at a more specific level and by comparing changes in colouration frequencies in several populations along phenotypic clines. In relation to immigration, it also remains largely unknown

whether different phenotypes for example represent different dispersal strategies. The mechanisms of phenotype-by-environment interactions and their impact on reproductive output could be investigated by cross-fostering experiments in different environments. Among others, pairing based on genetic compatibility (e.g. Tregenza and Wedell 2000, Oh and Badyaev 2006) or on the different behavioural traits of phenotypes (Ilyina and Ivankina 2001) may also contribute to the maintenance of phenotypic variation. Finally, processes acting on migration routes and wintering areas, such as context-dependent survival selection, may play a significant role in the persistence of phenotypic variation in the pied flycatcher.

In brief conclusion: this thesis suggests that there are a number of factors contributing to the maintenance of phenotypic variation in free-living populations. In general, varying contexts both in space and time seem to drive altering selection pressures and varying dispersal between locally adapted populations, which undoubtedly are important in maintaining phenotypic variation in the pied flycatcher and other free-living populations.

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